Statistical analysis of the phytocoenose homogeneity. IV. Species number and mean biomass value as functions of the area size

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Abstract

Homogeneity of the *Leocobryo-Pinetum* phytocoenose was assessed on the grounds of the effect of area size on the species number and mean biomass value. It was confirmed that: 1) species number was a logarithmic function of the area size; 2) relation of individual species biomass to the area size was, as a rule, other than rectilinear; 3) the size of phytocoenose floristically representative area differed from that determined with respect to the standing biomass and 4) phytocoenose homogeneity is related to the scale defined by the size of representative area.

Key words: phytocoenose homogeneity, minimal area, representative area

INTRODUCTION

Species number as a function of the area size has been an important aspect in the phytosociological analysis of phytocoenose homogeneity for a long time. Kylin (1926) has showed this relation to be of the logarithmic nature. Therefore theoretically, increase in the species number is unlimited and logarithmically proportional to the quadrat size. For long the fact whether empirical data fit this type of theoretical curve has been considered as the evidence of floristic homogeneity of the patch (Braun-Blanquet 1964).

In the early seventies Matuszkiewicz and Wydrzycka (1972) have conducted critical analysis of the relation of species number to the area size. They have discussed the problem in the context of phytocoenose homogeneity. The authors have thought that, although significant discrepancy

between empirical and theoretical values testifies to the phytocoenose non-homogeneity, agreement between them does not prove phytocoenose homogeneity. The problem should be further discussed.

The fact that species number depends on the area size implies the problem of minimal area. Now, its methodical aspect is mainly discussed — determination of the area representative for floristic composition of the phytocoenose (Matuszkiewicz and Wydrzycka 1972). It is analogous to the determination of representative sample in statistics. The area at which species composition least varies between different parts of the biochore can be considered as floristically representative for the analysed phytocoenose. Floristic composition in the representative areas can undergo only random changes.

The paper aims at: 1) analysis of homogeneity of the model phytocoenose on the grounds of the effect of area size on the species number and mean standing biomass, and 2) comparison of minimal areas determined with classical method of Braun-Blanquet (1964) and that of Calléja (1962). The fact whether species-area and biomass-area curves fit logarithmic function has been assumed as homogeneity criterion both for qualitative and quantitative measures.

The paper is the fourth in the series of works on the phytocoenose homogeneity. Their scope, aims and some results have been presented earlier (Kwiatkowska and Symonides 1985a, b, c). The studies were carried-out in the *Leucobryo-Pinetum* Mat. (1962) 1973 phytocoenose, with uniform physiognomy. It was composed of pure, even-aged, one-layered forest stand and floristically poor ground layer (21 species of vascular and 7 species of sporogenous plants) dominated by dwarf-shrubs. Floristic composition of the ground layer and interpopulational quantitative relationships have been presented in the first paper of the series (Kwiatkowska and Symonides 1985a).

MATERIAL AND METHODS

In sampling Greig-Smith's (1952) grid was used. It was composed of 512 square quadrats (sample areas) of side 1 m each. In the period of maximum standing biomass (July) in each quadrat all species were recorded. Then above-ground parts of all vascular plants in the ground layer were clipped and their air-dry biomass were assessed. The data were arranged in plans of species occurrence and cartogramms of their biomass in the successive quadrats. They served as a basis in the statistical analysis of phytocoenose homogeneity.

Species number-quadrat size relationship was analysed systematically with classical method (Braun-Blanquet 1964) and randomly with Calléja's

(1962) method. Both methods differed in sampling type and in that how they determined minimal area.

In the classical method the species number was determined in the runs of quadrats where each next quadrat included the former and was twofold bigger. Then, species-area curve was constructed in the arithmetic coordinate system. The area above which the curve became nearly horizontal was regarded as an indication of the minimal area.

In the paper four quadrat runs were determined. They were started from 1 m^2 quadrats in each corner of the grid (numbers 1, 16, 497 and 512, for the scheme see Fig. 1). Four replications enabled to assess effect

Fig. 1. Scheme of the increasing quadrat size in the classical, phytosociological method

of the species number in the first quadrat on the result of analysis. Next, values of differential quotient (rate of the species number increment to the increment of area size) were calculated. They formed the grounds for determination of the minimal area according to Calléja's (1962) formula, modified by Matuszkiewicz and Wydrzycka (1972). The differential quotient for minimal area equals 1.

Both, in classical and Calléja's methods runs of quadrats with geometrically increasing sizes were analysed. Mean species number calculated on the grounds of several random replications was considered characteristic of the

specified quadrat size. In the analysis quadrats with sizes ascending with geometric progression, from 1 to 128 m² (10 quadrats for each smaller size and all — 8 and 4 — for 64 and 128 m², respectively) were sampled without replacement.

Relation of the standing biomass of ground layer to the area size was elaborated analogously. Regression analysis of the standing biomass related to the area size included species with frequency not smaller than 20 per cent.

RESULTS

SPECIES NUMBER AS A FUNCTION OF THE AREA SIZE

The type of species-area relation is the same, independent of the method used (Figs. 2 and 3). It is a logarithmic function which fits regression equation $y = a \lg x + b$. Obtained curves differ only in values of a and b coefficients. The smallest a value is characteristic of the curve constructed on the grounds of mean species number (Table 1).

Table 1

Regression equations, correlation coefficients (r) and sizes of minimal area obtained in classical and Calléja's methods

Curve number	Regression equation	Correlation coefficient (r)	Minimal area, m ²
$\bar{x}$	$y = 1.8 \lg_2 x + 5.3$	0.99	3.03
1	$y_1 = 2.0 \lg_2 x + 2.7$	0.99	2.83
16	$y_{16} = 2.4 \lg_2 x + 4.8$	0.98	4.38
497	$y_{497} = 2.0 \lg_2 x + 4.0$	0.99	5.28
512	$y_{512} = 1.9 \lg_2 x + 3.3$	0.94	4.00

In the classical method value of "a" coefficient depends mainly on the species number in the first quadrat. Species richness of quadrats 16, 497, 512 and inter-relationships between quadrats with successively increasing sizes result in systematic increase in values of the analysed measure. When the first quadrat is poor in species, such as quadrat 1, systematic decrease in values takes place in the whole course of a curve.

All empirical values only slightly differ from regression lines. High value of correlation coefficient for the species number versus the area size (transformed logarithmically) shows it clearly (Table 1). Therefore, obtained

Fig. 2. Species-area relation in the classical, phytosociological method; 1, 16, 497, 512 — numbers of initial quadrats

Fig. 3. Species-area relation in Calléja's method

results related to the assumed criterion do not give grounds for rejection of the hypothesis on phytocoenose homogeneity.

Also differential quotient is similarly related to the area size in both methods used (Figs. 4 and 5). Both curves are hyperbolas. Moreover,

Fig. 4. Differential quotient as a function of the area size in the classical, phytosociological method; 1, 16, 497, 512 — numbers of initial quadrats

Fig. 5. Differential quotient as a function of the area size in Calléja's method. Broken line limits representative area

this constructed according to Calléja's method fits well theoretical curve (Fig. 5). On the other hand, the value of differential quotient depends on the method. It also differs between four curves obtained with classical method, such as in regression analysis.

The size of minimal area ranges between 2.8 m^2 and 5.3 m^2 for both methods (Table 1). Moreover, the range between the highest and

Fig. 6. Relation of ground-layer biomass to the area size in the classical and Calléja's methods

the lowest value obtained with the classical method includes the value of representative area (3 m^2) calculated on the grounds of mean species number.

STANDING BIOMASS OF THE GROUND LAYER AND THESE OF INDIVIDUAL SPECIES AS FUNCTIONS OF THE AREA SIZE

Regression analysis of the standing biomass versus the area size has proved that they are related rectilinearly, $y = ax \pm b$ type. Both in classical method and that of Calléja empirical curves differ from regression lines only insignificantly (Fig. 6). Value of correlation coefficient is always very high, in three cases exceeding 0.99 (Table 2).

Regression line constructed on the basis of mean ground-layer standing biomass lies in the area delimited by regression lines constructed according to the classical method. Two of them, $y = ax + b$ type, start in the area of high biomass values. Others, $y = ax - b$ type, start with quadrats with low biomass values. That all is reflected in the course of curves illustrating biomass increment for 1 m^2 . E.g. curves 1 and 16 for 1, 2, 4 and 8 m^2 are characterized by increase tendencies, i.e. decrease or increase in values of differential quotient of the ground-layer biomass (Fig. 7).

Table 2

Regression equations and correlation coefficients (r) for biomass-area relationship

Ground layer and species	Regression equation	Correlation coefficient (r)
Ground layer (linear approximation)	$y_{\bar{x}} = 37.3x + 13.2$	0.99
	$y_1 = 44.5x + 55.9$	0.99
	$y_{16} = 38.6x + 100.9$	0.99
	$y_{497} = 33.9x - 66.1$	0.99
	$y_{512} = 32.2x - 109.2$	0.99
Ground layer (logarithmic approximation)	$y_{\bar{x}} = 350.4 \lg_2 x - 361.1$	0.88
	$y_1 = 718.8 \lg_2 x - 1040.0$	0.88
	$y_{16} = 596.8 \lg_2 x - 767.5$	0.85
	$y_{497} = 508.4 \lg_2 x - 765.0$	0.83
	$y_{512} = 464.9 \lg_2 x - 710.8$	0.79
<i>Vaccinium myrtillus</i>	$y_1 = 35.9x - 13.7$	0.99
	$y_{16} = 30.2x + 112.8$	0.99
	$y_{497} = 4.0 \cdot 3.3^{\lg_2 x}$	0.97
	$y_{512} = 9.0 \cdot 2.5^{\lg_2 x}$	0.96
<i>Calluna vulgaris</i>	$y_1 = 64.4 \lg_2 x - 85.8$	0.90
	$y_{16} = 7.0 \lg_2 x - 8.3$	0.90
	$y_{497} = 63.3 \lg_2 x - 85.8$	0.88
	$y_{512} = 111.6 \lg_2 x - 85.0$	0.97
<i>Melampyrum pratense</i>	$y_1 = 6.8 \lg_2 x - 6.8$	0.90
	$y_{16} = 6.0 \lg_2 x - 4.4$	0.93
	$y_{497} = 0.45x - 2.7$	0.97
	$y_{512} = 0.25x + 0.6$	0.99

Theoretically, when relation is rectilinear, biomass increment should be constant, and straight line illustrating effect of the area size on this increment should be parallel to x -axis. From the curve analysis it can be inferred that the bigger quadrat size, the smaller amplitude of oscillations in the biomass increment for the unit area. It is most pronounced in the curve 16. Seemingly, it would indicate that standing biomass of the ground layer is related to the area size rather logarithmically than rectilinearly. However, empirical data do not fit so well regression lines when x variable (quadrat size) is transformed logarithmically. Also values of correlation coefficient are then lower ranging from 0.88 to 0.79 (Table 2).

It may be concluded that ground-layer biomass is directly proportional to the area size, whereas the phytocoenose is homogeneous with respect to the analysed measure.

Biomass of individual species is related to the area size in a different way. Only exceptionally relation is rectilinear, as in *Pinus sylvestris* or, for the classical method, in *Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L. (Fig. 8). Mostly regression equations are other than rectilinear.

In *Calluna vulgaris* (L.) Salisb. biomass is related to the area size mainly logarithmically (all curves obtained through the classical method) —

Fig. 7. Biomass increment per unit area as a function of the area size in the classical and Calléja's methods

$y = a \lg x - b$ (Fig. 8, Table 2). The curves differ between each other in values of: a coefficient (7.0-11.6), b coefficient (8.3-85.8), and correlation coefficient (0.88-0.97). It is determined, to a considerable extent, by biomass in the first and several successive quadrats. High biomass in the initial quadrat (quadrat 512) results in higher biomass values in the whole course of a curve, than when biomass in the first quadrat is low (quadrat 1 and 16, Fig. 8).

Fig. 8. Relation of individual species biomass to the area size; a — *Vaccinium myrtillus*, b — *V. vitis-idaea*, c — *Calluna vulgaris*, d — *Melampyrum pratense*, e — *Molinia coerulea*, f — *Pinus sylvestris*

For *Melampyrum pratense* L. two of the analysed relations — 1 and 16 — are of the logarithmic type $y = a \lg x - b$, while two others — 497 and 512 — are rectilinear, $y = ax \pm b$ (Fig. 8). In this case correlation coefficients are higher (0.90-0.99), than when all curves are assumed as logarithmic (0.80-0.93, Table 2).

Biomass of *Vaccinium myrtillus* is related to the area size rectilinearly ($y = ax \pm b$) or exponentially-logarithmically ($y = b a^{\lg x}$ Fig. 8, Table 2). Value of correlation coefficient is high, independent of the analysed relation: it exceeds 0.95.

Biomasses of *Calluna vulgaris* and *Melampyrum pratense* are not directly proportional to the area size, but to its logarithm. Consequently, mean

Fig. 9. Effect of the area size on estimation of individual species biomass per 1 m²; a-f as in Fig. 8

biomass value for 1 m² is different whether it has been calculated for small (1, 2, 4 m²) or big (16, 32, 64 m²) quadrats (Fig. 9). They both also differ from mean biomass value (straight line in Fig. 9), calculated for the whole grid. Especially large differences occur in curve 512 in *Calluna vulgaris* and curves 1 and 16 in *Melampyrum pratense* (Fig. 9).

Two tendencies have been noticed, independent of the type of biomass-area relation, namely: 1) ranges of values of standing biomass for 1 m², calculated on the grounds of 2, 4, 8, 16, 32 and 64 m² quadrats, decrease with the increase in the area size, and 2) the smallest oscillations in biomass value for 1 m² take place for the area size between 32 and 64 m² (Fig. 9).

Similarly, the value of biomass differential quotient for individual species depends on the quadrat size assumed in calculations (Fig. 10).

Fig. 10. Increment per unit area of the individual species biomass as a function of the area size; a-f as in Fig. 8

Discrepancy between empirical and theoretical straight lines is governed, besides random causes, by the type of biomass-area relationship.

In *Vaccinium myrtillus* relation is exponentially logarithmic. It results in an increase in the biomass differential quotient with a growth of the area size (curves 497 and 512, Fig. 10). For this and all other species the smallest amplitude of its oscillations is characteristic of large quadrats. When relation is logarithmic, such as in *Calluna vulgaris* and *Melampyrum pratense*, then biomass increment for the unit area decreases with increasing area size.

Differences in the value of differential quotient between four analysed curves are big for small quadrats, markedly decrease above 16 m² and become relatively constant for big quadrats.

The lowest amplitude of oscillations in values of differential quotients both for individual species and the mean ground-layer biomass per 1 m² appears in those calculated on the grounds of large quadrats — 32 and 64 m². Therefore it may be inferred that such quadrat sizes are already representative for the phytocoenose with respect to the analysed measure.

Plots with the same representative area size are similar to each other and least variable with respect to the analysed measure. The phytocoenose under study is homogeneous under the scale of its representative area.

DISCUSSION

Phytosociological analysis of the phytocoenose homogeneity has been often based on the assumption that observed data fit logarithmic type of species-area relationship (Braun-Blanquet 1928, 1964). It has been also commonly accepted that in a homogeneous phytocoenose species number is directly proportional to the area size.

Related to the species-area curve is a concept of minimal area (Hopkins 1957, Tüxen 1970). Various approaches of its determination have been always conventional (cf. Cain 1938, Archibald 1949, Du Rietz 1957, Braun-Blanquet 1964, Miyawaki and Ohba 1965, Tüxen 1970). Mostly, results of such studies are non-objective (as in the classical method where the position of area above which curve becomes nearly horizontal depends on the relative scales of ordinate and abscissa), demand the knowledge of the total species number in a phytocoenose (Archibald 1949), or eventually their scientific meaning is not established (Vestal 1949).

Therefore, the method where representative area is determined on the grounds of rate of increment of the species number to an increment of the area size is more appropriate. Although there are no premises why differential quotient equaled 1 should determine the size of representative area, but

then results of analysis are objective and unequivocal. Moreover, the size of representative area established according to Calléja's criterion is related to the scale of differentiation under which a phytocoenose is homogeneous (Calléja et al. 1962, Kwiatkowska 1972, 1984, Matuszkiewicz and Wydrzycka 1972). In the phytocoenose under study the size of floristically representative area agrees with that scale of spatial differentiation where most species are dispersed randomly (Kwiatkowska and Symonides 1985c).

Statistical criterion of homogeneity (Kylin 1926) is not closely related to the effect of area size on species number. The species number per unit area is a global characteristic. It is ecologically meaningful, especially when different phytocoenoses within the landscape, as well as different types of phytocoenose are compared. However, species number can be related not only to the whole phytocoenose, but also to its parts. Then, although its ecological interpretation is not so clear, frequency distributions of species number at different quadrat size can be analysed.

Calléja (1962) has proved that frequency distribution of species number per unit area is symmetrical and fits the normal distribution, independent of the area size. Therefore, it is probable that just this measure, among other phytocoenose features, always meets the condition of statistical homogeneity.

In the classical method species-area curve is constructed analogously to the construction of cumulative series for the species number. As distribution mentioned above is symmetrical, analysed relation must be a logarithmic function. However, curve related to cumulative series may be logarithmic not only for random distributions.

It may be concluded that species-area relationship better shall not be assumed as criterion of phytocoenose homogeneity because: 1) it cannot be unequivocally ecologically interpreted, at least under some scale of spatial differentiation of vegetation; 2) it is not directly related to the statistical criterion of homogeneity; 3) phytocoenose which is homogeneous with respect to the type of frequency distribution of species number per unit area, and where species number is related to the area size logarithmically, may be non-homogeneous with respect to other measures.

Sizes of the representative area obtained according to classical and Calléja's methods are similar (3-5 m²). Moreover, in both methods species-area relationship is logarithmic. However, values of analysed measures vary between replications in the classical method and between both methods.

Regression analysis of the ground-layer biomass related to the area size has shown this relation to be rectilinear, independent of the method used. However, results of the classical method are not obvious; frequency distribution of biomass is symmetrical (fits the normal distribution) only for 8 and 16 m² (Kwiatkowska and Symonides 1985b).

Analysis of the relation between individual species biomass and the area size gives more interesting results. For many species relation is more complex than rectilinear. Biomass-area relation can be logarithmic, or with power and logarithmic components. Chojnacki (1974) has obtained similar results for herbs and dwarf-shrubs in the *Leucobryo-Pinetum* phytocoenose, variant with *Molinia coerulea*. There he has randomly taken samples of different size.

From comparison of analysis results where systematic (classical method) and random (Calléja's method) sampling have been used it may be concluded that individual species biomass is related to the area size non-linearly. Discrepancies between curves of biomass differential quotient and hypothetical straight line, parallel to X-axis also indicate that.

The fact that in all analysed species mean biomass value per 1 m², calculated on the grounds of successive quadrats differs from theoretical constant value, is also worth noting. Differences between four analysed replications are non-random. E.g. mean biomass value per 1 m² decreases or increases with increasing quadrat size, i.e. it is directly or inversely proportional to the area size.

Summing-up, results of the classical method with respect to individual species biomass depend on the position of initial quadrat. Also derivative functions such as: biomass differential quotient and mean biomass value per 1 m² related to the area size differ between replications.

Obtained results indicate contagious spatial organization of the analysed measure. Therefore, the type of biomass-area relationship depends on the mode of sampling (cf. Kwiatkowska and Symonides 1985a, c). Parts of analysed phytocoenose differ from each other in spatial organization of species biomass, so replications which characterize parts of the grid also differ in the type of function and values of equation coefficients. When biomass-area relation is not rectilinear, such function cannot indicate spatial homogeneity. On the other hand, in the analysed phytocoenose the scale of spatial differentiation, where biomass differential quotient and mean biomass value per 1 m² are least variable, can be distinguished. Such area is representative from statistical point of view (Kwiatkowska and Symonides 1978a, b, 1980).

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Statystyczna analiza jednorodności fitocenozy. IV. Liczba gatunków i średnia wartość biomasy jako funkcja wielkości powierzchni

Streszczenie

Praca jest częścią szerszych studiów nad problemem homogeniczności fitocenozy, mających na celu porównanie wyników uzyskanych dla cech jakościowych i ilościowych, z zastosowaniem różnych wskaźników homogeniczności. We wcześniejszych opracowaniach miarą jednorodności

był rozkład wskaźników ogólnej różnorodności gatunkowej i równomierności (Kwiatkowska i Symonides 1985a), rozkład frekwencji i rozkład wartości biomasy jako funkcja wielkości powierzchni (Kwiatkowska i Symonides 1985b) oraz rozkład przestrzenny gatunków i ich biomasy jako funkcja wielkości powierzchni (Kwiatkowska i Symonides 1985c). Do badań wytypowano fizjonomiczne jednorodny płat *Leucobryo-Pinetum* Mat. (1962) 1973, szczegółowo opisany w pierwszej pracy cyklu (Kwiatkowska i Symonides 1985a).

W niniejszej pracy przeprowadzono analizę homogeniczności badanej fitocenozy na podstawie typu zależności liczby gatunków od wielkości powierzchni i typu zależności wartości biomasy od wielkości powierzchni. Jako kryterium jednorodności przyjęto zgodność krzywej obu zależności z funkcją logarytmiczną. Celem pracy było ponadto porównanie wielkości powierzchni minimalnej wyznaczonej metodą klasyczną (Braun-Blanquet 1964) i metodą Calléja (1962).

Badania wykazały, że: 1) zależność liczby gatunków od wielkości powierzchni jest taka sama, niezależnie od zastosowanej metody; liczba gatunków jest logarytmiczną funkcją wielkości powierzchni (rys. 2 i 3); 2) w obu metodach zależność ilorazu różnicowego od wielkości powierzchni ma charakter funkcji hiperbolicznej (rys. 4 i 5); 3) wielkość powierzchni minimalnej obliczona metodą klasyczną i Calléja jest podobna (tabela 1); 4) niezależnie od metody wartość biomasy runa zmienia się wprost proporcjonalnie do wielkości powierzchni (rys. 6), a wahania wartości przyrostu biomasy na jednostkę powierzchni dla poszczególnych poletków są losowe (rys. 7); 5) zależność stanu biomasy poszczególnych gatunków od wielkości powierzchni najczęściej nie jest prostoliniowa, przy czym funkcje typu logarytmicznego lub wykładniczo-logarytmicznego najlepiej aproksymują dane empiryczne uzyskane metodą klasyczną; 6) w skupiskowym rozmieszczeniu biomasy poszczególnych gatunków i nieliniowej zależności stanu biomasy od wielkości powierzchni tkwi przyczyna różnej oceny średniej wartości badanej cechy na 1 m^2 (rys. 9); 7) wahania wartości ilorazu różnicowego biomasy poszczególnych gatunków nie są losowe i wraz ze wzrostem wielkości powierzchni rosną lub maleją, zależnie od sposobu rozmieszczenia ich biomasy na obszarze biochory (rys. 10).

Reasumując stwierdzono, że homogeniczność fitocenozy odnosi się do skali określonej wielkością powierzchni reprezentatywnej. Badania wykazały jednak, iż wielkość powierzchni reprezentatywnej florystycznie różni się od wielkości powierzchni reprezentatywnej pod względem stanu biomasy.